

"WE'LL MEET AGAIN", AN EXPRESSION REMARKABLY APPLICABLE TO THE HISTORICAL BIOGEOGRAPHY OF AUSTRALIAN ZODARIIDAE (ARANEAE)

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The largest subfamily of the Zodariidae, the Zodariinae, contains 31 genera and has endemic representatives on all tropical continents. The sequence in this clade first indicates that the Australian zodariid fauna is the result of a combination of vicariance and dispersal events. Only three zodariid genera are not endemic to Australia. It is argued that two of these, *Mallinella* and *Asceua*, have reached Australia by dispersal over forest-covered areas. It is remarkable that the endemic Australian genera in the Zodariinae are more closely related to the African ones than are the Neotropical genera which is in contrast with the current ideas on chronology in plate tectonics. A possible explanation might be found in the past and present distribution of forests. The appearance of this type of vegetation on the Cretaceous-Tertiary boundary, might also be invoked to explain bipolar distributions in Africa.

La plus importante des sous-familles des Zodariidae, les Zodariinae, contient 31 genres, dont des endémiques sur chaque continent tropical. La séquence dans ce grand clade indique d'abord que la composition de la faune australienne serait le résultat d'une combinaison de vicariance et de dispersion. Seuls trois genres trouvés en Australie n'y sont pas endémiques. On avance l'argument selon lequel deux d'entre eux ont réussi à atteindre l'Australie par dispersion à travers des aires couvertes de forêts. Il est remarquable que les genres endémiques australiens soient plus proches des genres africains que de ceux d'Amérique du Sud ce qui contredit les idées courantes concernant la chronologie de la dérive des plaques. Une explication possible pourrait se trouver dans la distribution passée et actuelle des forêts équatoriales. La genèse de ce type de végétation, à la fin du Crétacé, pourrait également expliquer la distribution bipolaire de certaines vieilles lignées d'invertébrés. □Africa, Gondwanaland, distribution, vicariance.

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The Zodariidae are a medium-size pantropical family of mainly nocturnal, ground-living spiders. Except for the members of the subfamily Storenomorphinae they are virtually all burrowers to some degree. Some simply dive into sand (*Psanmoduon*) or hide in litter (*Asceua*, *Mallinella*) whereas others make a complex retreat consisting of a burrow with a trapdoor (*Psanmorygma*, *Neastorena*) or an igloo-like construction of pebbles or grains of sand (*Diores*, *Zodarion*). This sedentary lifestyle and the fact that zodariids do not balloon explains why most species have small distribution ranges. It also makes them an ideal subject for zoogeographical studies, moreover since a cladistic analysis of the family is available (Jocqué, 1991).

THE AUSTRALIAN ZODARIIDAE

Most Australian zodariids, estimated at several hundred species, belong to genera endemic to the Australian continent. There is no trace of any

Genus	Distribution	Habitat
<i>Asceua</i>	Palaeotropics & Australia	circumforest
<i>Asteron</i>	Australia	steppe-woodland
<i>Cyrioctea</i>	southern Gondwana	dunes
<i>Habronestes</i>	Australia	steppe-woodland
<i>Ishunia</i>	South and Central America	circumforest
<i>Mallinella</i>	Palaeotropics & Australia	tropical forest
<i>Neastorena</i>	Australia	steppe-woodland
<i>Storena</i>	Australia	steppe-woodland
<i>Storosa</i>	Australia	steppe-woodland
<i>Teneidus</i>	South and Central America	steppe-circumforest

TABLE 1. Distribution and habitat of some zodariid genera.

representatives of these genera on any other continent (Table 1).

Three genera have representatives elsewhere and in fact have the centre of their distribution outside Australia. The first one is *Cyrioctea*, the only genus in the Cyriocteninae, found exclusively in sandy habitats such as arid dunes and sand deserts. It has a typical Gondwanan distribution



FIG. 1. Approximate distribution of *Mallinella*.

with representatives in South Africa, Chile and Australia (*Cyrioclea raveni* Platnick and Griffin). Both the other genera, *Mallinella* and *Asceua*, have an enormous distribution which appears to be linked with old world forests. One species of each has reached the northern tip of Australia.

The Australian zodariid fauna is thus apparently composed of three different stocks: a strictly endemic one, a southern Gondwanan one and a third element that could be quoted as old world forest fauna. To understand this composition we have to go back to an era before the breakup of Gondwanaland.

The Zodariidae indeed have a basic Gondwanan distribution with the more plesiomorphic taxa represented in Africa, Australia and South America. These are the Cyriocleinae, the Lachesaninae and the more plesiomorphic members of the Zodariinae. The latter taxon is now known to include what has been described as the subfamily Storeninae (Jocqué, 1991, 1992). Thirty-one out of 47 genera now belong in the Zodariinae. However, the more apomorphic members of the subfamily (Femoral Gland Clade or FGC), having several synapomorphies (femoral gland, lack of chilum, flattened incised hairs, fused chelicerae) are present only in Africa (including part of the Palaearctic) and tropical Asia. The same applies to the Storenomorphinae and the Cydreliinae which are restricted to tropical Africa and tropical Asia.

When Africa got finally separated from other major landmasses, slightly more than 100 mybp, these three groups were apparently not yet in existence. The bulk of the zodariid fauna outside that continent is therefore supposed to be derived of the plesiomorphic taxa present at the time of the split-off. However, from the above it is clear that India (and part of South East Asia ?) carried a much more modern assemblage of Zodariidae when it moved towards its present position. Indeed, there is no evidence that at least purely

tropical forest organisms (e.g., *Mallinella*) originating in Africa, have been able to reach India via a northern itinerary. No forest connection has ever existed via the mediterranean and the Arabian peninsula. This paradox is discussed below.

Virtually all Zodariidae are restricted to habitats lying in a climatic zone with a marked dry season. In the Neotropics only a few species (in *Ishania* and *Tenedos*) seem to have adapted to moist forest and no zodariids have so far been found in Amazonia. In Australia no true forest-inhabiting species belonging to endemic genera appear to be present, although some species in the genera *Neostorena*, *Asteron*, *Storosa* and *Habronestes*, occur in dense woodland. But the most common and widely distributed forest inhabiting genus is doubtlessly *Mallinella*. This genus has an enormous distribution (Fig. 1): it occurs in virtually all African forests from Senegal in the west to the Chimanimani Mts. (Zimbabwe) (Jocqué, unpublished data) in the south and Kenya and Ethiopia in the east, but is remarkably absent from the South African forests which emphasizes its inability to cross unforested zones. It is present in montane rainforest in India and Nepal and occurs in virtually all dense forests in the Far East, as far as New Guinea. One species has reached the northeastern tip of Australia. This is apparently a very recent event as that species, *Mallinella zebra* Thorell, occurs on both New Guinea and Australia. Considering the fractionating of this genus in the rest of its distribution range and the fact that no speciation has occurred in this case, there is little doubt that the arrival occurred during the Pleistocene ice-ages, during which there was a land-bridge linking New-Guinea and Australia (Keast, 1983). A well documented case of a less recent Asian invader is that of *Tamopsis* (Hersiliidae) which is supposed to have arrived in northern Australia during the Miocene (Baehr, 1988). This relatively early arrival has resulted in clockwise colonization of almost the entire circumference of the Australian continent and the appearance of many strongly related species.

A second recent zodariid arrival is that of an undescribed species of *Asceua* (Jocqué, in preparation) which can be characterized as a circum-forest genus. Its ecological status is fairly similar to those genera mentioned above, which occasionally occur in dense woodland or even rainforest in the case of the South American *Ishania* and *Tenedos*. The distribution of *Asceua* (Fig. 2) is even larger than that of *Mallinella* and

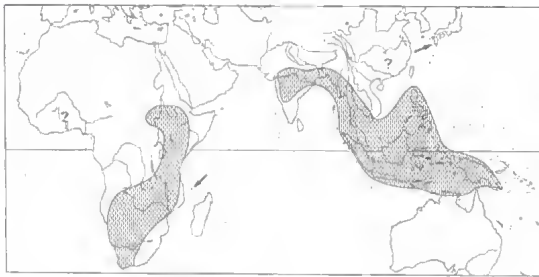


FIG. 2. Approximate distribution of *Asceua*.

the patterns overlap only partially. Although several Asian species are known to occur in rainforest (Bosmans and Hillyard, 1990; P. Schweninger pers. comm. 1989; C. Deeleman-Reinhold, pers. comm. 1988; J. Murphy, pers. com. 1988) no representatives are found in African lowland rainforest. On the other hand it is present in rather dry areas in southern Africa. Considering its very restricted distribution area in Australia, it is supposed to have arrived there at the same time as *Mallinella*.

Two closely related lines of zodariines which had been separated for about a hundred million years thus met again.

Assuming that *Mallinella* was initially better adapted to rainforest conditions, it would be interesting to study if the arrival of *Mallinella zebra* has induced a shift in the rest of the zodariid fauna in the area it now occupies, and whether it is still expanding.

GENERAL DISTRIBUTION OF THE ZODARIINAE

The monophyletic assemblage of the Zodariinae is largely composed of genera which are endemic to particular continents (Jocqué 1991, fig. 41). Remarkably, the African genera are apparently more closely related to the Australian Zodariinae than to those in South America. The five Neotropical genera are indeed near the root of the zodariine branch whereas the Australian ones are situated in between the Afrotropical and the Palaeotropical ones (the latter group has an apparently recent outflow into the Palaeartic). The reduced area-cladogram resulting from these relationships is given in Fig. 3. This statement is at least puzzling: it is in contrast with the timing of major plate tectonic events that caused the breakup of Gondwanaland, as deduced from geological data and corroborated by many biogeographical data (e.g.

Nelson and Platnick, 1980). However, not only is there much controversy about the original position of many plates, the timing and the mechanics of the movement are also subject to a debate. The expansion theory of Carey (1975) and Shields (1979, 1983) positions several plates in different places than does the classical theory (Norton and Sclater, 1979; Owen, 1983). According to the latest data (Veevers *et al.*, 1991; Scotese *et al.*, 1988; Powell *et al.*, 1988) it appears that India split off from Gondwanaland together with the southern continents Australia and Antarctica. How then can one explain the fact that India and Sri Lanka share many apomorphic monophyletic taxa with Africa (e.g., *Hermippus*, Storenomorphinae, Cydrelineae, members of the FGC)? Briggs (1987) thinks that India, on its course to Asia, became again attached to north-east Africa by the end of the Cretaceous, a remarkable hypothesis that might explain the apparent faunal anomaly. It would certainly explain how forest dwelling spiders like *Mallinella* and *Asceua* have reached Asia.

The main question that is raised by the zodariid cladogram is why the Australian taxa are more strongly related to the African than to the South American ones.

A possible explanation is that the few typical forest inhabiting zodariid genera did only evolve after the main continents had broken away from Africa. Broad-leaved forests arose at least during the Cretaceous but became dominant in equatorial conditions on the Cretaceous-Tertiary boundary (Wolfe, 1987; Wolfe and Upchurch, 1986, 1987). It is strange that in the context of African biogeography no mention has been made of the dramatic shift that has been brought about by the appearance of broad-leaved evergreen forest. The conditions at ground level in this kind of forest and the former conifer forests were probably as different as they are for instance in present-day rainforest and miombo in Africa. The faunas of these vegetation types are equally very different. Dense miombo woodland and submontane evergreen forest within each other's sight on the Nyika Plateau in Malawi, contain completely different litter-layer spider faunas with hardly any genus overlap in the spider families that have been studied (Zodariidae, Linyphiidae, Lycosidae, Tetragnathidae; Jocqué, unpublished data).

The present day bipolar distribution of many ancient African taxa of ground-dwelling invertebrates might therefore be explained in the light of the evolution of broad-leaved rain forest

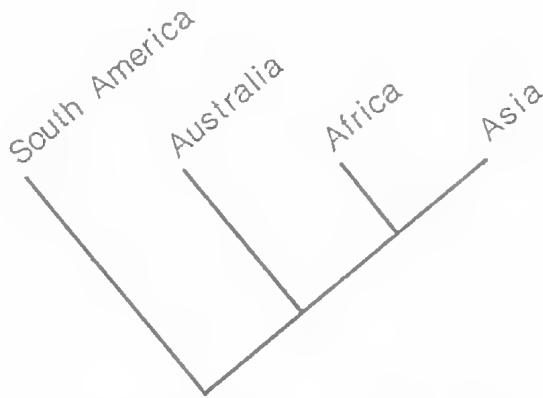


FIG. 3. Area cladogram of tropical continents as based on the clade of the Zodariinae.

during the Cretaceous. This novel type of vegetation with a very new structure and hence ecological conditions, split most existing taxocoenoses that had to adapt to the new forest conditions. In the Zodariidae only very few genera succeeded in doing so. In Africa only *Mallinella* really developed into a specialised forest spider genus.

The remote relationship of South American and African Zodariidae may well be the result of similar events at the time of the breakup of Gondwanaland favouring the dispersion of particular genera, hampering that of others.

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